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THE MECHANISM OF EVOLUTION

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IV. MENDELIAN INHERITANCE

THE factors of development, whether of an individual or of a species are both intrinsic and extrinsic, hereditary and environmental; but every evolutionary change must be inherited else it would be ever-changing and evanescent; consequently only inherited changes in organisms are of evolutionary value. The chief problems of evolution concern the manner of origin and fixation of these inherited changes. Nearly thirty years ago Osborn said: "When we have reached an inheritance theory that will explain the facts of heredity the problem of the causes of evolution will be a thing of the past."[1] We have now reached a theory of inheritance that explains the main facts of heredity and both directly and indirectly it has contributed enormously to the solution of the evolution problem. But although certain phases of that problem are now things of the past many new phases have appeared which are still unsolved.

The history of Mendel's discovery and the principles of Mendelian inheritance have been described so frequently of late that it is not necessary to dwell upon them here. In bare outlines the essential features of this theory and of later additions to it may be summarized as follows:

1. ALTERNATIVE INHERITANCE

Sexually produced organisms are mosaics of characters each of which is usually derived from one or the other of the two parents but not from both. These alternative characters or their germinal factors are known as allelomorphs. For example, Mendel found that when two varieties of peas are crossed, one having yellow seeds (Y) and the other green (G), all hybrids of the first generation (F_1), had yellow seeds but with green recessive or latent, Y(G), as was shown by the fact that when each of those hybrids was self-fertilized it produced a second generation (F_2) which formed yellow and green seeds in the proportion of three yellows to one green (3Y : 1G). In subsequent generations (F_3, F_4, etc.), if flowers were self-fertilized, green seeds always gave rise to plants with green seeds, one third of the yellow seeds produced plants which bore only yellow seeds, while two thirds of them produced plants which bore yellow and green seeds in the proportion of three to one (3Y : 1G) as in the second hybrid generation. The whole result may be summarized in the following scheme:

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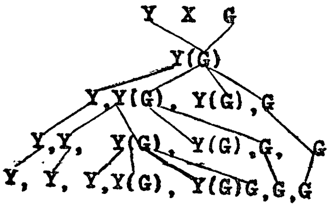
[1] Osborn, H. F., "Evolution and Heredity," Woods Hole Lectures, 1891.

Parent Generation (P)—
First Filial Generation (F_1)—
Second " " (F_2)—
Third " " (F_3)—
Fourth " " (F_4)—
Etc.



That is green-seeded plants always breed true when self-fertilized, those which are pure yellow-seeded also breed true, while those which are hybrid yellow and green with the green recessive, Y(G), give rise in each generation to yellow-seeded and green-seeded plants in the proportion of 1Y : 2Y(G) : 1G.

Mendel found that the same principle held true of several other contrasting characters or allelomorphs such as round (R) and wrinkled (W) seeds, tall (T) and dwarf (D) stems, etc. In every case he found that the first hybrid generation resembled one parent only with respect to any of these contrasting characters and these characters he called *dominant* while those which became latent or hidden in the hybrid he called *recessive*. In some cases hybrids are more or less intermediate between the parents and in such neither character completely dominates the other; thus Correns found that when

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[2] All kinds of germ cells, whether plant or animal, male or female, are known as gametes and the union of male and female gametes gives rise to the zygote, which is the fertilized egg or the organism into which it develops. When two gametes with the same hereditary constitution unite they produce a *homozygote* or pure-bred individual; when gametes of different constitution unite they produce a *heterozygote* or hybrid. All the gametes produced by a homozygote are of the same hereditary type, those produced by a heterozygote are of two different types for each pair of contrasting characters of the parents. The various types of hereditary constitution, such as are indicated by YY, Y(G), GG in this table are known as *genotypes;* the types of developed organisms are *phenotypes.* Thus the three genotypes named constitute only two phenotypes since YY and Y(G) give rise to developed organisms which look alike.

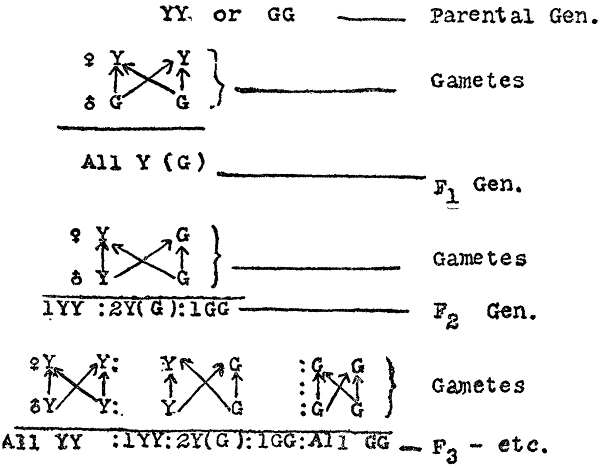
a white-flowered variety of *Mirabilis,* the "four o'clock," was crossed with a red-flowered variety all of the hybrids of the F_1 generation had pink flowers and from these in the F_2 generation there came white-flowered, pink-flowered and red-flowered forms in the proportion of 1 white; 2 pink; 1 red. This is a better illustration of the Mendelian law than is offered by the peas, since in this case the hybrids are always distinguishable from the pure dominants.

When peas with two contrasting characters are crossed only the dominant characters appear in the F_1 generation but in subsequent generations every possible combination of these characters occurs. Thus when peas with yellow and round seeds (YR) are crossed with green and wrinkled (GW) the F_1s are all yellow and round-seeded, but with green and wrinkled recessive, Y(G)R (W), and these, when self-fertilized, yield 9YR : 3YW : 3GR : 1GW in the proportions named.

When peas with three contrasting characters are crossed, one having yellow and round seeds and tall stem, (YRT) with one having green and wrinkled seeds and dwarf stem (GWD) all hybrids of the first generation have yellow and round seeds and tall stem, the other characters being recessive, Y(G)R(W)T(D); but when these hybrids give rise to the second hybrid generation (F_2) all possible combinations of these original characters appear, and in the following proportions:—27RYT : 9RYD : 9RGD : 9WYT : 3RGD : 3WYD : 3WGT : 1WGD. These characters are therefore separable in heredity; they behave as separate units in hereditary transmission and are therefore called "unit characters."

Purity of Germ Cells.—Mendel clearly perceived that there must be things in the germ cells which corresponded to or gave rise to these characters in the developed plant and, although he represented these things by letters, he did not attempt to define or describe them. It was evident that these things or factors or *genes* as they are now called were separable in heredity and that every germ cell, even though it came from a hybrid, could carry the genes for only one of each of these contrasting characters. Thus the hybrid produced by crossing green with yellow-seeded peas must form equal numbers of two kinds of germ cells, one carrying the gene for green seeds and the other that for yellow. No germ cell could carry both of these genes and this led to the most important of the Mendelian discoveries, namely that in the formation of germ cells there is a separation or segregation of genes so that every germ cell is "pure" with respect to the genes for any two contrasting characters.

Consequently when a germ cell carrying the gene for green (G) is fertilized by another carrying the same kind of gene (G) a pure bred green-seeded plant results (GG) ; when a germ cell carrying the gene for yellow (Y) is fertilized by another carrying a similar gene (Y) a pure yellow-seeded plant is produced (YY) ; but when a germ cell carrying the gene for yellow (Y) unites with one carrying the gene for green (G) a hybrid carrying both genes results, Y(G), the yellow gene however being dominant over the green. All the germ cells of a pure green-seeded plant carry the green factor, all those of a pure yellow-seeded plant carry the yellow factor, but half of the germ cells of a hybrid between yellow and green-seeded plants carry the factor for green and the other half the factor for yellow. Consequently since in the last named case these two kinds of germ cells are produced in equal numbers there is one chance in four that two germ cells with the yellow factor will unite or that two with the green factor will unite while there are two chances in four that a germ cell carrying the yellow factor will unite with one carrying the green factor. All this may be summarized in the following scheme:



Monohybrids, Dihybrids, Trihybrids, etc.—When parents differ in only a single pair of contrasting characters, as in yellow or green seeds, round or wrinkled seeds, tall or dwarf stem the resulting offspring are monohybrids; where they differ in two pairs of characters the offspring are dihybrids; where they differ in three pairs they are trihybrids, and where they differ in more than three pairs of characters the offspring are polyhybrids.

When the parents differ in only one pair of contrasting characters or allelomorphs, one of which completely dominates the other in the F_1 hybrids, there are in the F_2 generation 3 genotypes and 2 phenotypes, or developed types, in the relative number of 3 dominants to 1 recessive; this is the simple Mendelian or monohybrid ratio. When the parents differ in two, three or more such characters the number of types and their ratios are the square, cube, etc. of those for the monohybrid, as shown in the following table:

Number of Genotypes and Phenotypes when there are from 1 to 7 Pairs of Allelomorphs

Pairs of Allelomorphs	Number of Genotypes in F_2	Phenotypes in F_2	
		Number	Ratios
1	$(3)^1=3$	$(2)^1=2$	$(3:1)^1 = 3:1$, *i. e.*, 1 phenotype (of 3 individuals): 1 phenotype (of 1 individual)
2	$(3)^2=9$	$(2)^2=4$	$(3:1)^2 = 9:3:3:1$, *i. e.*, 1 phenotype (of 9 individuals): 2 phenotypes (of 3 each): 1 phenotype (of 1 ind.)
3	$(3)^3=27$	$(2)^3=8$	$(3:1)^3 = 27:9:9:9:3:3:3:1$, *i. e.*, 1 (27):3(9):3(3):1(1)
4	$(3)^4=81$	$(2)^4=16$	$(3:1)^4 = 81:27:27:27:27:9:9:9:9:9:9:3:3:3:3:1$, *i. e.*, 1(81):4(27):6(9):4(3):1(1)
5	$(3)^5=243$	$(2)^5=32$	$(3:1)^5 = 1(243):5(81):10(27):10(9):5(3):1(1)$
6	$(3)^6=729$	$(2)^6=64$	$(3:1)^6 = 1(729):6(243):15(81):20(27):15(9):6(3):1(1)$
7	$(3)^7=2187$	$(2)^7=128$	$(3:1)^7 = 1(2187):7(729):21(243):35(81):35(27):21(9):7(3):1(1)$

Where there are many allelomorphs the possible number of genotypes and phenotypes, due to different combinations, becomes very great and the relative numbers of the different phenotypes differ widely. In almost every case parents differ in more than a single character and in many cases, such as species crossings, they differ in a great many characters. It would not be possible to determine experimentally the absolute and relative numbers of different types in such cases without an enormous number of offspring. Fortunately it is usually possible to deal with each pair of contrasting characters by itself and without regard to the others so that, in such a case, one determines for each pair of characters whether they occur in the simple Mendelian ratio of 3 : 1.

Thus not only the different combinations which are possible but also the relative numbers or ratios of these different combinations are all explained by the simple principle of the "purity" of a germ cell with respect to any given gene and the chance union of germ cells in fertilization. *This is undoubtedly one of the greatest discoveries ever made in the field of biology and it is as far-reaching in results as it is simple in principle.*

This principle of the separableness of inheritance factors or genes in hereditary transmission has been demonstrated in hundreds of cases in both plants and animals and there is now no reason to doubt that it is a universal law of heredity. The many apparent exceptions to this law which were noted when the Mendelian discovery was new have been shown to be due to misunderstandings of the principles involved, or to unwarranted emphasis upon certain minor phases of Mendel's theory, or to a failure to properly analyze the characters in question or their causes.

The Factorial Theory of Heredity.—Germinal factors or genes are not wholly independent things though they may be localized in the chromosomes and may be separated, transposed and recombined in sexual reproduction. Furthermore it is not true that genes are merely the developed characters, in minute form, or that the factorial theory merely shifts the mysteries of heredity from the region of visible characters to that of invisible factors. Genes are not undeveloped characters but rather the elements whose combinations and interactions produce developed characters, just as combinations of chemical elements produce chemical compounds or as combinations of cells produce tissues and organs. The properties of the compounds or organs or characters are not to be found as such in the elements or cells or genes which enter into their genesis but they result from the combination or synthesis of these elements. Morgan says that each gene probably influences many characters and that it may possibly influence every character of the developed organism, and on the other hand it is known in certain instances that more than one gene is concerned in the production of a particular character. But while it is true that one gene may influence many characters and that more than one gene may be concerned in the production of a given character it is generally true that a particular gene is the *differential factor* in the production of any particular character. Very many factors are involved in the production of a white or red flower, of a white or black guinea pig, but in each case there is at least one factor which is *differential,* that is it is found in one of these alternatives and not in the other. This differential factor alone is emphasized in dealing with the hereditary causes of these differences,—it is sometimes spoken of as if it were the only factor or gene concerned in the production of the character, whereas all that is meant is that it is the differential factor.

Multiple Factors.—When more than one gene is concerned in the development of a character the factors or genes are said to be multiple. Thus in many instances the development of color is dependent upon two or more separable factors, and only when all of these factors are present does color develop typically. A similar condition is usually found in the inheritance of size, and gradations in size or color may be explained as the result of varying combinations of these multiple factors.

Modifying Factors.—Akin to cases of multiple factors are those conditions in which the action of a principal factor is modified by subordinate factors. Morgan and Bridges have discovered six or seven such factors which modify the "Eosin" eye color of *Drosophila*. These modifying factors are also separable in heredity and the stronger or weaker development of certain characters can be shown to depend upon certain combinations of these modifying factors. The fact that selection may serve to build up or to reduce a character is known to be due in some instances to the selection of individuals with or without certain of these modifying factors.

Lethal Factors.—Finally Morgan and his associates have demonstrated the existence of a considerable number of lethal factors in *Drosophila* which cause the early death of those gametes or zygotes in which such a factor is not balanced by a normal one. Consequently only heterozygotes with respect to such lethal factors survive and all individuals which are homozygous for a lethal factor usually die so early that they are never seen. Nevertheless their existence can be determined by indirect methods, such as linkage with sex. Such lethal factors modify expected Mendelian ratios and greatly complicate the study of genetics, but they do not destroy its fundamental principles, indeed when properly understood they furnish one of the strongest proofs of the truth of the factorial theory of heredity.

The factorial theory is as necessary to the study of heredity as is the atomic theory to the study of chemistry and the one is as well justified by the results obtained as is the other. Weismann says that for a long time he tried to avoid the assumption of the existence of inheritance factors, but he finally came to the conclusion that no understanding of the phenomena of heredity was possible on any other basis. At present inheritance factors are no more hypothetical than are atoms and electrons. We know not only that they exist but also that they are located in the chromosomes; we know how they are separated and recombined in sexual reproduction and we know that evolution is caused in some cases at least by changes in these factors or genes.

2. BLENDING INHERITANCE

When the Mendelian theory was new it was generally supposed that there were forms of inheritance which differed materially from the Mendelian type; in fact it was supposed that the latter was one of the less common forms of heredity and that blending of parental traits and not separation was the rule. Among such cases of blending inheritance may be mentioned the color of hybrids of white-flowered and red-flowered "four o'clocks" and of white and black men, the size of hybrids of large and small races of rabbits or other organisms, etc. In these cases the F_1 generation is more or less intermediate between the two parents but the significant fact, which was formerly overlooked, is that in the F_2 and subsequent generations we have a more or less complete segregation of the original characters out of these hybrids in which the characters are blended. In the F_2 generation the pink-flowered "four o'clocks" produce white-flowered and red-flowered as well as pink-flowered plants, the children of mulattoes range in color from white to black, the offspring of those hybrids which are intermediate in size between their parents are large and small and intermediate. In these cases there is a true Mendelian segregation of genes but owing to the fact that one gene does not completely dominate its allelomorph or to the fact that multiple factors are present in varying numbers the hybrid is intermediate between the two parents.

Other cases of apparent blending inheritance are found in quantitative characters in which the size of offspring or the degree or extent of their pigmentation ranges all the way from one parental type to the other. Such cases have been studied particularly by Castle in rabbits and in hooded rats and he concluded that such intergrades could not be explained by the segregation of constant genes but must be attributed to quantitative and qualitative changes in the genes themselves. MacDowell, on the other hand, showed that in rabbits the intergrades in size may be explained more satisfactorily by the multiple-factor hypothesis than by Castle's hypothesis of changes in the genes themselves. And the work of Morgan and his associates on the gradation of eye-color in *Drosophila* has shown that such gradations are due to "modifying factors" which increase or diminish the action of the principal factor.

Castle has more recently accepted this principle of modifying factors as an explanation of the results of his work. There are then in all these cases several factors which are concerned in the production of these quantitative characters and the intergradations which occur are due to varying combinations of these factors rather than to modifications of the factors themselves. Blending inheritance, therefore, so far from being a contradiction of the Mendelian principle of the segregation of unchanging factors, becomes an important argument in favor of that principle.

3. SPECIES HYBRIDS

a. Numerous Allelomorphs.—In species crosses certain phenomena occur which do not appear to be Mendelian in character. For example, species hybrids are usually intermediate between the two parents so that it looks as if this were a case of blending inheritance. This appearance may be due to the large number of dominant factors which are contributed by each parent so that in general the offspring seem to be intermediate; or it may be due to the fact that neither allelomorph of a pair completely dominates the other in which case there should be a segregation of parental characters in the F_2 generation. In the classical cases of Mendelism the varieties crossed differ in only a few characters. Linnean species, however, differ in very many characters and if the dominant characters are pretty equally distributed between the two species the result would be that the hybrids would appear to be intermediate. This is in fact one of the most general features of hybrids between species. If such intermediacy is really the result of the combination of large numbers of contrasting characters, or rather of their genes, the F_2 generation should present a large number of segregations and therefore wide variability. Owing to the large number of contrasting characters or allelomorphs in different species the number of possible combinations in the F_2 generation is very great (p. 174) and immense numbers of offspring are necessary in order to determine whether or not all these possibilities are realized and still larger numbers are needed to determine the *relative* numbers of these different types.

Thus the *smallest* number of offspring which would represent the Mendelian ratios of different types, where one allelomorph completely dominates the other, would be for

1	pair	of	Allelomorphs,	4	F_2	individuals.
2	"	"	"	16	"	"
3	"	"	"	64	"	"
4	"	"	"	256	"	"
5	"	"	"	1,024	"	"
6	"	"	"	4,096	"	"
	Etc.					

Of course a much greater number than that must actually be observed if the ratios are to be determined with any approach to accuracy. For example, in determining the simple 3:1 ratio in the cross of yellow-seeded and green-seeded peas, Mendel observed 6,022 yellow seeds and 2,001 green seeds and 15 different investigators who have made this cross have recorded in the F_2 generation a total of 152,824 yellow-seeded to 50,676 green-seeded peas which makes the ratio 3.004: .0996 or very nearly 3:1. (See Morgan, 1919, p. 24.) It would therefore be an enormous labor to determine with any accuracy the relative numbers of different types which would result where there were even five or six pairs of allelomorphs.

For example, Baur has determined the existence of more than 20 different factors for the color and form of flowers in the snap-dragon *Antirrhinum*. Lotsy crossed two species of snap-dragon, *A. majus* × *A. molle;* the F_1 hybrids were intermediate in all respects and were completely fertile; out of an F_2 population of 255 plants, he distinguished about 25 different flower types, besides many other character differences such as size, form of leaf, habit of growth, etc. One of these F_2 plants produced 209 plants of the F_3 generation all of which had different types of flowers, but wherever single pairs of allelomorphs could be recognized and followed it was found that their segregation in the F_2 and subsequent hybrid generations approximated the Mendelian ratio of 3:1.

Detlefsen obtained essentially similar results in crossing two different species of the guinea pig, *Cavia porcellus* × *C. rufescens*. He studied in particular five pairs of contrasting characters in the color and arrangement of the hair and as a result of this work he concludes that in the hybrids of these species inheritance is Mendelian.

b. Infertility.—But another and even greater difficulty in determining whether species-crosses are Mendelian or not results from the fact that such hybrids are frequently but not invariably more or less infertile. If certain combinations of allelomorphs should be sterile or less fertile than others it would cause wide departures from the expected ratios and in cases where infertility of hybrids is the rule, it is of course impossible to determine whether or not Mendelian segregation occurs. There are however many cases in which such hybrids are fertile and in all such cases there are evidences that inheritance is Mendelian. On the whole there is no good reason to suspect that species-crosses differ fundamentally from variety-crosses in this respect.

4. UNEQUAL RECIPROCAL HYBRIDS

In typical Mendelian inheritance reciprocal crosses yield identical results. Thus it does not matter in a cross between white and red guinea pigs whether the male is white and the female red or *vice versa;* the results are the same in either case. But in some instances reciprocal crosses yield different results. Thus the cross between the male ass and the female horse yields a mule, but the reciprocal cross between the female ass and the male horse produces a hinney. When the hybrid resembles the father more than the mother it is said to be "patroclinous"; when the reverse is true it is "matroclinous." Such unequal reciprocal hybrids have been studied especially in the Œnotheras by de Vries and he comes to the conclusion that they are due to the fact that the male and female gametes of a species may carry different factors—that they may be heterogamous as contrasted with the more usual conditions where they are isogamous. The cause of heterogamy is obscure, but de Vries suggests that the pollen which receives maternal factors, for example, may remain rudimentary so that all the active pollen carries only paternal factors while the reverse may be true of the egg cells.

The extensive work which Morgan and his associates have done on lethal factors in *Drosophila* shows that they play an extremely important part in the non-survival of certain gametes or zygotes. They have demonstrated that a number of such lethal factors are located in the X chromosome and that all individuals in which such a factor is not balanced by a normal allelomorph die early. All males that receive such a factor die since there is only one X chromosome in the male; all females that receive it in both X chromosomes die, while only those survive that have such a lethal factor in one or neither of the X chromosomes.[3]

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[3] Bridges has shown also that patroclinous sons and matroclinous daughters may result from a phenomenon which he calls "non-disjunction," that is the failure of certain pairs of chromosomes to separate during the maturation of the germ cells.

In some such manner as this it may be possible to explain the condition of heterogamy and unequal reciprocal hybrids. Such hybrids therefore do not disprove the Mendelian law but they furnish additional and unexpected support for it when they are properly analyzed. We may therefore conclude that the Mendelian law of heredity, especially as regards the segregation of inheritance factors, is of universal occurrence—that there is no other type of inheritance.